Research paper

Relationships of tree height and diameter at breast height revisited: analyses of stem growth using 20-year data of an even-aged *Chamaecyparis obtusa* stand

Akihiro Sumida[1,4], Tomiyasu Miyaura[2] and Hitoshi Torii[3]

[1]Institute of Low Temperature Science, Hokkaido University, N19W8, Sapporo 060-0819, Japan; [2]Faculty of Science and Technology, Ryukoku University, Seta Oe-cho, Otsu, Shiga 520-2194, Japan; [3]Chita Shoyo High School, Dougashima, Yawata, Chita, Aichi 478-0001, Japan; [4]Corresponding author (asumida@lowtem.hokudai.ac.jp)

Stem diameter at breast height (DBH) and tree height (H) are commonly used measures of tree growth. We examined patterns of height growth and diameter growth along a stem using a 20-year record of an even-aged hinoki cypress (*Chamaecyparis obtusa* (Siebold & Zucc.) Endl.) stand. In the region of the stem below the crown (except for the butt swell), diameter growth rates (ΔD) at different heights tended to increase slightly from breast height upwards. This increasing trend was pronounced in suppressed trees, but not as much as the variation in ΔD among individual trees. Hence, ΔD below the crown can be regarded as generally being represented by the DBH growth rate (ΔDBH) of a tree. Accordingly, the growth rate of the stem cross-sectional area increased along the stem upwards in suppressed trees, but decreased in dominant trees. The stem diameter just below the crown base (D_{CB}), the square of which is an index of the amount of leaves on a tree, was an important factor affecting ΔDBH. D_{CB} also had a strong positive relationship with crown length. Hence, long-term changes in the D_{CB} of a tree were associated with long-term changes in crown length, determined by the balance between the height growth rate (ΔH) and the rising rate of the crown base (ΔH_{CB}). Within the crown, ΔD's were generally greater than the rates below the crown. Even dying trees ($\Delta D \approx 0$ below the crown) maintained $\Delta D > 0$ within the crown and $\Delta H > 0$ until about 5 years before death. This growth within the crown may be related to the need to produce new leaves to compensate for leaves lost owing to the longevity of the lower crown. These results explain the different time trajectories in DBH–H relationships among individual trees, and also the long-term changes in the DBH–H relationships. The view that a rise in the crown base is strongly related to leaf turnover helps to interpret DBH–H relationships.

Keywords: allometry, crown rise, linear mixed models, pipe model theory, stem form, stem taper.

Introduction

The relationship between trunk diameter at breast height (DBH) and tree height (H) is the most commonly used measurement of tree size. The allometric relationship of DBH and H among individuals at a particular point in time (hereafter: static DBH–H allometry) has long been used to describe the strategies of tree species (e.g., Hara et al. 1991, Sterck and Bongers 1998, Osunkoya et al. 2007, King et al. 2009, Iida et al. 2011).

However, there are still uncertainties in the use of static DBH–H allometry for ecological studies. For example, long-term changes in static DBH–H allometry among trees have not agreed with the time trajectories of DBH–H relationships of individuals in the stand (Kohyama et al. 1990, Sumida et al. 1997). In annual plants, the discrepancy between static diameter–height allometry and time trajectories can be explained by the observation that time trajectories vary among plants

according to the plants' competitive status within a stand (Weiner and Thomas 1992, Nagashima and Terashima 1995). Dominant plants have linear diameter–height trajectories while suppressed plants have curved trajectories, with diameter growth declining more than height growth. However, it is not clear if these observations for annual plants are applicable to tree species because the growth of trees continues for years by continuously increasing both diameter and height. Hence further studies are required to determine the DBH–*H* relationships in tree species (Henry and Aarssen 1999).

Another issue to consider when determining the DBH–*H* relationship in trees is the use of DBH to represent diameter growth along a stem. Growth patterns, as recorded by DBH, do not always represent stem-mass growth patterns (Bouriaud et al. 2005, Sillett et al. 2010), probably because diameter growth rates along a stem are often particularly large in the upper part of the stem (Courbet and Houllier 2002) and around the crown (Funada et al. 1989). Discriminating stem shapes in a tree between the region within the crown and the region below the crown base is important in stem shape studies because the region within the crown is more tapered than the region below the crown (Gray 1956, van Laar and Akça 2007).

The strongly tapered stem within the crown is closely related to the progressive increase in the cumulative amount of leaves downwards from the treetop. The amount of leaves above a given location of the stem is nearly proportional to the cross-sectional area of the stem at that location (Shinozaki et al. 1964a). This constitutes the basis of the assumption used in several models of tree growth that the border between one model equation and another (except for butt swell) corresponds to the location of the base of the crown (Valentine and Gregoire 2001, Valentine and Mäkelä 2005).

For the region of the stem below the crown, Larson (1963) summarized studies reported since the 19th century and found that, in closed even-aged stands, trees with a crown having close neighbors, but not overtopped, displayed approximately equal cross-sectional area growth within a stem but annual-ring width decreased downward from the crown base, whereas trees that were overtopped and with relatively small crowns displayed a downward decrease in both area growth and ring width. This description accords with studies incorporating stem mechanical theories, in that diameter growth below the crown should decrease downward from the crown base, although allometric equations for expressing stem shape may vary among studies (McMahon 1975, Oohata and Shinozaki 1979, Chiba 1990, Morgan and Cannell 1994, Niklas 1995, West et al. 1997, Mäkelä 2002, Valentine et al. 2012).

As a physiological basis for enabling these growth patterns along a stem, plant hormonal activities are considered to be relevant (Larson 1963). Although there are still uncertainties in its exact role (e.g., Uggla et al. 1996, 1998, Nilsson et al. 2008), the activity of an auxin (indole-3-acetic acid, IAA) is considered to be important for radial growth because the vertical distribution of cambial growth along a stem, and therefore the diameter growth rate, accords with the distribution of IAA activities (Funada et al. 2001). Indole-3-acetic acid activity is known to be high in the crown, and the region of activity in a stem varies among trees according to the difference in the ratio of crown length to the total stem length (Uggla et al. 1998). Hence crown length has also been suggested to affect cambial growth along a stem (Funada et al. 1989).

Crown-base height is important for reasons other than the expression of the vertical position of the crown base. According to the pipe model theory (Shinozaki et al. 1964a), the square of the diameter of the stem just below the crown base (D_{CB}: hereafter referred to as the crown-base diameter) is directly proportional to the amount of leaves on an individual tree (Shinozaki et al. 1964b). The pipe model is widely accepted as a method for estimating the amount of leaves on a tree from the crown-base diameter (Mäkelä 2002, Sumida et al. 2009).

Note that as tree height increases with growth, the crown base also rises (i.e., it increases in height) owing to natural pruning of the branches in the lower part of the crown in a closed stand (Osawa 1990, Oliver and Larson 1996, Sumida and Komiyama 1997). Thus, the height of the probable border of stem taper and diameter growth patterns should increase with crown rise. However, changes in crown-base diameter associated with crown-base rise have been considered in only few studies of stem diameter growth (e.g., Osawa 1990, Ilomäki et al. 2003, Mäkelä and Valentine 2006, Valentine et al. 2012), perhaps because the tree growth data required for such studies are difficult to obtain. Estimating past crown-base heights, and hence stem diameters at the crown base, for an adequate number of sample trees is almost impossible with the most commonly used stem analysis method. For this reason, previous studies have had to incorporate several assumptions into their analyses (e.g., Chiba et al. 1988, Osawa et al. 1991, Valentine et al. 1994, Ilomäki et al. 2003, Valentine and Mäkelä 2005).

Considering the previous studies discussed above, the crown-base rise which may accompany changes with time in the crown-base diameter, or the amount of leaves on a tree, could be used to clarify uncertainties in DBH–*H* relationships. To address this, we used an intensively measured 20-year tree inventory data set that enabled the analyses of the following: (i) patterns of diameter growth rates at different locations along a stem, including DBH growth rates, (ii) relationships among height growth, crown-base rise and changes with time in the amount of leaves on a tree using the record of the crown-base stem diameter as an index of the amount of leaves per tree (Shinozaki et al. 1964b), and (iii) time trajectories of DBH–*H* relationships for individual trees, and the relationship between the time trajectories and the changes with time in

static DBH–H allometry. A possible physiological mechanism that could generate resultant diameter growth patterns along a stem is further discussed.

Materials and methods

Study sites and field measurements

The study site was an even-aged plantation of hinoki cypress (*Chamaecyparis obtusa* (Siebold & Zucc.) Endl.) in the Experimental Forest of Nagoya University at Inabu, Aichi Prefecture, Japan. This species is native to Japan where its timber is of great value, whereas in Europe and North America it is cultivated as an ornamental tree (Phillips 1978). In reserves in Japan, the largest *C. obtusa* live >300 years in their native environment (Hoshino et al. 2001) and the maximum tree height is 20–30 m (Kitamura and Murata 1979). Dense branches with flattened, scale-like leaves spread horizontally without forming branch whorls, and the crown becomes rounded in old trees (Hayashi 1985). This relatively shade-tolerant species grows slowly, and the forest floor below its canopy is dark (generally 5–10% of full sunlight; see Appendix A in Niinemets and Valladares 2006). At our study site, the average relative light intensity on the forest floor was <4% (Miyaura and Hozumi 1982).

The study plot covered 191 m² and was located ~970 m a.s.l., on a steep slope (average 37°) facing northwest (35°12′14″N, 137°33′58″E). The stand was 21 years old when established as a study plot in 1977. In this paper, stand age and tree age are assumed to be the same. No artificial thinning or branch pruning had been conducted in the study plot since the saplings were planted, and therefore tree growth was dense. The population consisted of 142 live trees (~7400 ha^{-1}) in 1977, which had decreased to 92 (~4816 ha^{-1}) in 1996 (40 years old) as a result of self-thinning. The estimated values of leaf area index (LAI) of the study plot in 1974 (18 years old, 3 years before the beginning of this study) and in 1981 (25 years old) were 5.38 and 5.93 m² m^{-2}, respectively; LAI was estimated by applying allometric relationships obtained by sampling trees in a stand near the study plot (Hagihara et al. 1978, Miyaura and Hozumi 1982). The mean tree height and mean crown-base height (see below for exact definitions) increased from 7.4 to 12.2 m and from 3.1 to 7.4 m, respectively, from 1977 to 1996. See Table S1 available as Supplementary Data at *Tree Physiology* Online and Miyaura and Hozumi (1985) for further stand information.

All data obtained for this study were collected using non-destructive measurements. For all live trees in the plot, we recorded tree height (H, m), crown base height (H_{CB}, m) which was measured as the height of the lowest live branch of a tree, and stem girth at the crown-base height, which was measured just below the lowest live branch. The girths of the stem at 0 m (stem base) height, 0.3 m height, and at 1-m intervals from

0.3 m height to the interval nearest the treetop were recorded each year for 19 years (or 20 year-by-year records) from 1977 (stand age, 21 years) to 1996 (stand age, 40 years). The crown length of a tree for a given year (CL, m) was defined as the difference between tree height (H) and crown-base height (H_{CB}). All data are available in Supplementary File 1 available as Supplementary Data at *Tree Physiology* Online.

The stem location at 1.3 m height was initially marked on each tree to allow measurements at the same location in different years. The positions for girth measurements at heights >1.3 m were determined as the distance from the 1.3 m height location measured each year, using plastic or steel tape, by climbing trees using a monopole ladder or by climbing scaffolds built in the plot. Girths at each measurement point were measured using steel tape and recorded to the nearest 0.1 cm. For tree height, we climbed to the treetop and measured the length along the stem between the 1.3-m mark and the treetop using a plastic tape. Tree heights (stem length) were determined to the nearest 1 cm, although the probable maximum measurement error of tree height was ±5 cm, especially in cases when dense branches made it difficult to pull the tape along the stem within the crown. The crown-base height (H_{CB}) was identified each year by a tag attached to the lowest live branch of a tree, and rise in the crown base was determined by the death of the branch with a tag attached in a previous year. Measurements were made in late autumn each year when diameter and height growth during the growing season had ceased (Paembonan et al. 1990).

All girth records were converted to diameter or cross-sectional area in this study, assuming a circular stem cross section. The stem girth at the crown base was also converted into crown-base diameter (D_{CB}, cm). In the *C. obtusa* stands around the study plot, D_{CB} has been reported to exhibit a strong allometric relationship with the amount of leaves on an individual tree (Miyaura 1989, Hagihara et al. 1993), supporting the validity of the pipe model of tree form (Shinozaki et al. 1964a, 1964b). Hence, D_{CB} was used as an index of the amount of leaves on a tree. The stem cross-sectional area at the crown base A_{CB} (cm²) was calculated by $A_{CB} = D_{CB}^2\pi/4$.

Statistical analyses

Linear mixed model analyses were used to test for the effects of possible influences on diameter growth rate or on cross-sectional area growth rate at different locations on a stem. Location on a stem (L_{CB}, m) for an individual tree in each year was expressed as the distance from the crown base ($L_{CB} \equiv$ crown base height − given stem height). Hence, $L_{CB} > 0$ for stem locations below the crown base, and $L_{CB} < 0$ within the crown. Diameter growth rate (ΔD, cm year^{-1}), or the stem cross-sectional area growth rate (ΔA, cm² year^{-1}), at a given stem location for a given individual tree during calendar year Y and $Y + 1$ were the response variables in the linear mixed

models. L_{CB}, ΔD and ΔA did not include data for stem locations at heights ≤1.3 m. For each of the two response variables, DBH growth rate (ΔDBH, cm year^{-1}) or the growth rate of stem cross-sectional area at breast height ΔABH (cm^2 year^{-1}) between Y and $Y + 1$, stem location (L_{CB}) at Y, and their interaction term ($L_{CB} \times \Delta$DBH or $L_{CB} \times \Delta$DBH) were employed as fixed-effect explanatory variables in the full model. The calendar year 'Y' was treated as a random effect in this analysis because a preliminary examination indicated that the calendar year was likely to have affected the diameter growth rate as an external factor, randomly changing from year to year, rather than simply expressing the progress of time or the aging of trees. In addition, the tree identification number (ID) was incorporated as another random-effect explanatory variable because preliminary analyses showed that models with the tree ID as a random effect (i.e., the ID number was treated as qualitative variable) were generally better (in terms of Akaike's information criterion (AIC); see below) than models without this variable. This was probably because the microenvironments of trees, such as the presence of nearby neighbors, larger neighboring trees and the occasional death of neighboring trees, affected the growth of different trees of similar sizes as an unknown effect, which is often treated as a random effect (Faraway 2006). Possible combinations of the explanatory variables including their interaction terms were tested, and the best model was selected using AIC. For the linear mixed model analyses, the function 'lmer' of the package 'lme4' (Bates et al. 2011) from the statistics package R version 2.13.0 Patched (R Development Core Team, 2011) was used.

The mixed model analyses were conducted separately for the region of the stem within the crown and for the region of the stem below the crown. Diameters recorded within 1 m from the top of a tree and diameters <1 cm were excluded from all statistical analyses because stem morphology near the top of the tree was often irregular, largely owing to the difficulty of differentiating between leaves and stems. Diameter/growth data at the stem base (height = 0 m) and at 0.3 m height were also excluded from the mixed model analyses, as the formation of the stem shape of the butt swell was not considered in this study.

Results

Diameter growth observed in the stem profiles of individuals

When the 20-year stem profiles were preliminarily reconstructed for each of the trees using our inventory data, the profiles varied substantially among trees (see Supplementary PDF 1 available as Supplementary Data at *Tree Physiology* Online). Figure 1 shows the stem profiles of three representative trees, which had different overall changes with age in crown-base stem diameter D_{CB} (horizontal locations of closed circles in Figure 1). Among all the trees that had survived for 40 years, these examples were selected because the slope of the regression between D_{CB} and age was the largest (Figure 1a), the closest to zero (Figure 1b) and the smallest (i.e., negative, Figure 1c).

For all three trees, the changes in D_{CB} were generally accompanied by an increase in the crown-base height H_{CB} with age. This crown-base rise accounted for the differences in the stem profiles between the trees. The crown-base location (closed circles) in each year appeared to correspond to the border of changes in the diameter growth rates along a stem in intermediate (Figure 1b) and weakly growing (Figure 1c) trees, such that each year's diameter increment was lower below the crown base. This trend indicates that the diameter growth rate
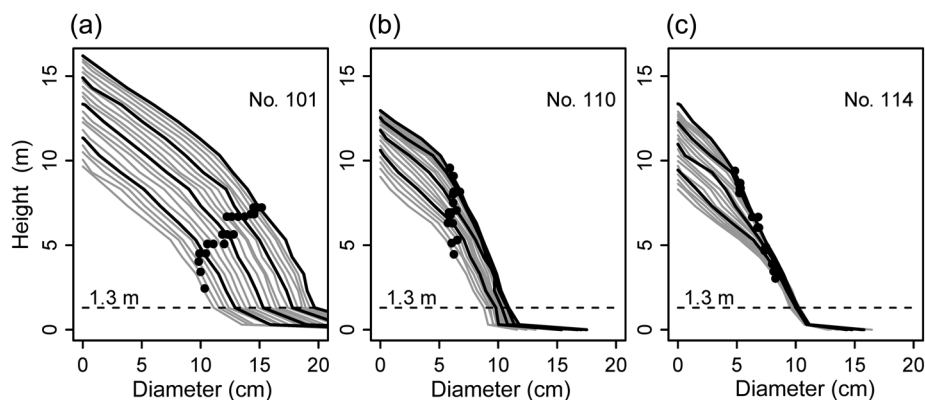

Figure 1. Examples of stem profiles for three trees (tree nos. 101, 110 and 114) with different patterns of changes with age in crown-base diameter D_{CB}. In each tree, the stem shape for each year from 21 to 40 years old was reconstructed from non-destructive measurements of stem diameters and tree height. Thick lines show stem shapes at 5-year intervals. Filled circles show the crown-base location, with the vertical location of each circle indicating the crown-base height H_{CB} of each year, and its horizontal location representing the crown-base stem diameter D_{CB} of each year. The slopes of the regression between D_{CB} and age were (a) 0.296 cm year^{-1} (t value = 21.23, $P < 0.001$; $n = 20$, $R^2 = 0.960$) for tree no. 101, (b) 0.001 cm year^{-1} (t value = 0.115, $P > 0.5$; $n = 20$, $R^2 = 0.000$) for tree no. 110, and (c) −0.200 cm year^{-1} (t value = −15.06, $P < 0.001$; $n = 20$, $R^2 = 0.922$) for tree no. 114. See Supplementary PDF1 available as Supplementary Data at *Tree Physiology* Online for results for all trees in the plot.

at a given stem height decreased after that stem height shifted from the region within the crown to the region below the crown, due to crown-base rise. In particular, in tree no. 114, in which D_{CB} displayed a decreasing trend (Figure 1c), diameter growth below the crown base was very weak over the 19 years. Clearly, a decrease in the amount of leaves on a tree over time, as indicated by D_{CB}, can occur irrespective of increasing DBH.

When stem diameter growth rates (ΔD) of trees were compared with the DBH growth rate (ΔDBH) for all trees by pooling all data, data points within the crown were mostly scattered above the 1 : 1 line (Figure 2a), indicating that ΔD was greater than ΔDBH within the crown. Such a trend is not conspicuous in the region below the crown base (Figure 2b).

Diameter at breast height growth rates were positively related to both DBH (Figure 3a) and D_{CB} (Figure 3b). The latter relationship indicates that the amount of leaves on a tree was
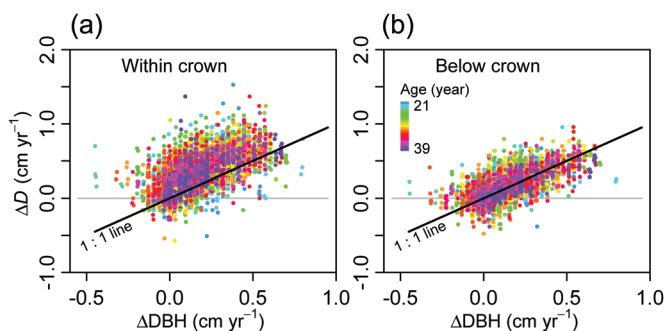
an important factor in DBH growth. Slopes of these regression lines tended to become gentler in each advancing year, probably as data ranges of DBH and D_{CB} increased with age without notably changing the data ranges of ΔDBH (Figure 3).

Diameter and cross-sectional area growth along a stem

To further explore how diameter growth rates varied along a stem in relation to the crown base locations, ΔD values at all stem locations measured on all trees over the 19 years were plotted against the stem location from the crown base (L_{CB}) of the respective years (Figure 4a). In Figure 4a, ΔD data for trees with a similar ΔDBH (indicated by similar symbol colors) did not markedly vary with stem location in the region below the crown, as indicated by the similar symbol colors being scattered horizontally.

The results of the best models determined from the linear mixed model analyses are shown graphically in Figure 4c. The equations of the lines were obtained by substituting ΔDBH values that were the 99th, 90th, 50th, 10th and 1st percentiles of all ΔDBH values for all trees during the 19 years of observation, into the fixed effects parameters of the best models in Table 1. The results of the random effects (calendar year 'Y' and tree identification number 'ID') are presented in Table S2 available as Supplementary Data at *Tree Physiology* Online. As shown in Figure 4c, the fixed-effect curves representing the percentiles of ΔDBH fairly separated the exemplary data points representing each ΔDBH rank. The fixed-effect curves shows that, in the region below the crown, trees with a greater ΔDBH (≥90th percentile) had a slight increase in ΔD as the stem location was closer to the crown base. This increasing trend in the fixed-effect curves was pronounced in trees with a lower ΔDBH. In contrast, ΔD within the crown progressively increased towards the treetop in all trees (Figure 4a and c).

Changes in stem cross-sectional area growth rates (ΔA) along a stem exhibited a different pattern from that of ΔD (Figure 4b). This difference was because ΔA at a stem location calculated with a given ΔD also depends on the stem diameter at that stem location. The results of linear mixed model analyses are presented in Table 2 and Table S3 available as Supplementary Data at *Tree Physiology* Online and are shown graphically in Figure 4d. In the region below the crown, trees with moderate and small ΔABH (≤50th percentile) had an increased ΔA with stem height towards the crown base, but those with a large ΔABH (≥90th percentile) had a decreased ΔA with stem height (Figure 4b and d). Hence the difference in ΔA and ΔABH ($\Delta A - \Delta ABH$) was negative in trees with a large ΔABH and positive in trees with a small ΔABH (Figure 4f). Such a tendency was, however, not pronounced in the case of ΔD (Figure 4e). Within the crown, in contrast to the trends observed in ΔD, ΔA tended to decrease towards the treetop in many trees, probably because stems become thinner in this region.

Figure 2. Relationships between diameter growth rates (ΔD) of a tree and its DBH growth rate (ΔDBH) for (a) the region within the crown and (b) the region below the crown. All annual growth data for 19 years (growth rates from 21–22 to 39–40 years old) were plotted, and colors show tree age. The black solid line in each figure indicates the 1 : 1 line. See Figure 4c for the regression between ΔD and ΔDBH together with stem location information.
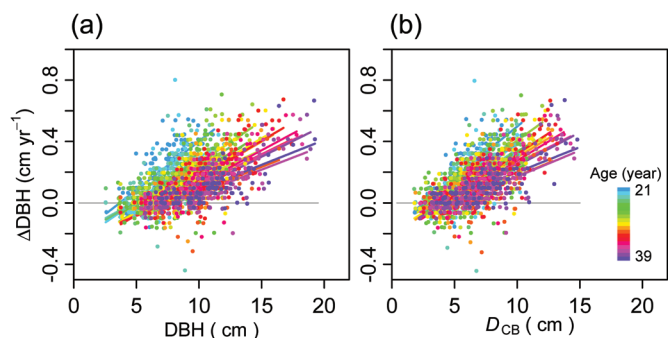

Figure 3. Relationships of DBH growth rates (ΔDBH) with (a) DBH and (b) crown-base stem diameter (D_{CB}). ΔDBH between ages Y and $Y + 1$ were plotted for DBH or for D_{CB} at age Y for trees living at age $Y + 1$. Regression analyses were performed for each of 19 years of growth (growth rates from 21–22 to 39–40 years old). Regressions were significant for all years in both (a) and (b) (all $P < 0.001$; other statistical results are omitted). Colors of data points and regression lines show tree age.
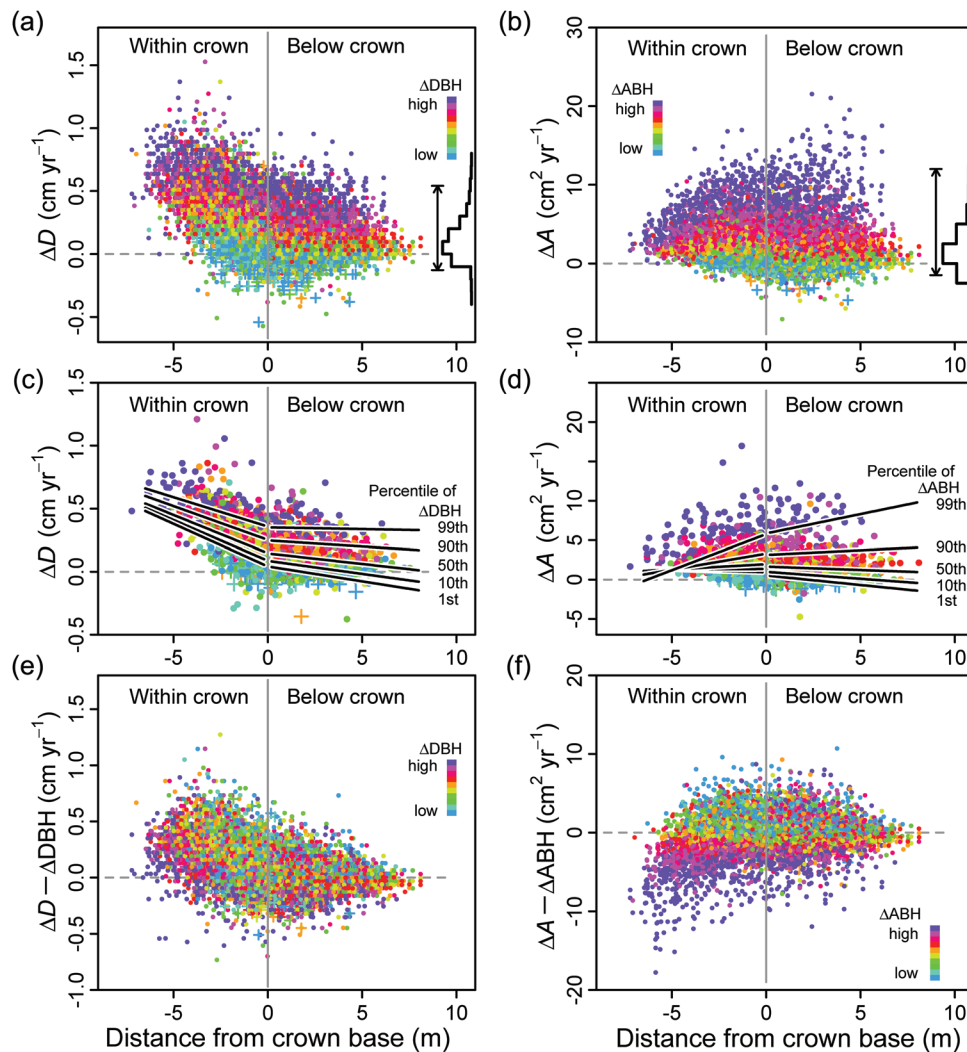
Figure 4. Patterns of diameter growth (left column) and cross-sectional area growth (right column) along with stem locations (L_{CB}) expressed as distance from the crown base of each tree in each year. (a) ΔD plotted against L_{CB}. (b) ΔA plotted against L_{CB}. In (a) and (b), all living trees in each of the 19 years were sorted into ten ranks according to (a) DBH growth rates (ΔDBH) and (b) cross-sectional area growth rates at breast height (ΔABH), respectively, and are shown by different colored symbols. The frequency of ΔDBH (a) or ΔABH (b) of all the trees is illustrated on the right side by pooling all data for 19 years, and the arrows near the frequencies show the range of their percentiles between 5th and 95th. (c) Changes in ΔD with L_{CB} for trees with ΔDBH percentiles (by pooling all data for 19 years) of 99th, 90th, 50th, 10th and 1st, which corresponded with ΔDBH = 0.541, 0.318, 0.095, −0.032 and −0.127 cm year^{-1}, respectively. Lines were drawn by substituting these values to the equation shown below Table 1. (d) Changes in ΔA with L_{CB} for trees with ΔABH percentiles as in (c). The percentiles corresponded with ΔABH = 12.00, 5.11, 1.37, −0.30 and −1.48 cm^2 year^{-1}, respectively, and lines were drawn by substituting these values into the equation shown below Table 2. In (c) and (d), exemplary data points are shown by choosing data for a tree that had an intermediate (median) rate of ΔDBH (c) or ΔABH (d) within each of the 10 growth levels (i.e., the 10 colors) in each year. (e) Difference in ΔD values of a tree from ΔDBH of each tree ($\Delta D - \Delta$DBH) in each year. (f) Difference in ΔA values of a tree from ΔABH of each tree ($\Delta A - \Delta$ABH) in each year. The color of symbols in (e) and (f) are the same as in (a) and (b), respectively. Data for trees that died before 40 years of age (the dying trees) are denoted by ' + ' symbols in (a), (b), (e) and (f).

Long-term changes in crown length and crown-base diameter

The stem profiles in Figure 1 illustrated that tree-height growth (increase in H) and crown-base rise (increase in H_{CB}) occurred simultaneously in each tree. To understand this pattern of crown-base rise in individual trees in relation to the trees' height growth patterns, the crown length of each tree in the initial year of observation (21 years old: CL_{21}) was compared with that in the final year (40 years old: CL_{40}) for all trees in the plot.

From Figure 5a, it can be seen that trees with longer crown lengths in the initial year (CL_{21}) tended to increase their crown length more by the final year (CL_{40}), although the slope of the regression line (solid line) did not significantly differ from unity ($P = 0.055$). Nevertheless, of the 50 trees that died before 40 years of age (hereafter 'the dying trees': open symbols in Figure 5a), 37 trees were positioned below the gray 1 : 1 line, indicating that crown lengths decreased before their death (one-tailed binomial test: $P < 0.001$). Note that this decrease

Table 1. Results of fixed effects of the linear mixed model shown in Figure 4c. The response variable was the annual growth rate of stem diameter (ΔD, cm year^{-1}) at a given stem location for a tree in a year. The fixed effects of explanatory variables are stem length from crown base (L_{CB}, m; $L_{CB} \equiv$ crown base height − given stem height) and DBH growth rate (ΔDBH, cm year^{-1}) of each tree in each year.

Explanatory variable	Estimate	Standard error	t value
(a) Region within the crown			
Intercept	0.102	0.017	5.83
Length from crown base (L_{CB})	−0.064	0.004	−14.84
DBH growth rate (ΔDBH)	0.472	0.049	9.58
$L_{CB} \times \Delta$DBH	0.043	0.015	2.80

AIC of the selected model was −7801, which was lower than that of the second-best model by ΔAIC = 4. Total number of data points was 7071.

(b) Region below the crown			
Intercept	0.101	0.010	10.23
Length from crown base (L_{CB})	−0.020	0.002	−11.90
DBH growth rate (ΔDBH)	0.462	0.023	19.86
$L_{CB} \times \Delta$DBH	0.031	0.004	7.77

AIC of the selected model was −19,775, which was lower than that of the second-best model by ΔAIC = 22. Total number of data points was 10,098.

Using the estimates above, the equations for the lines in Figure 4c are expressed as follows:
Region within the crown: $\Delta D = 0.102 − 0.064 \times L_{CB} + 0.472 \times \Delta$DBH$ + 0.043 \times (L_{CB} \times \Delta$DBH$)$.
Region below the crown: $\Delta D = 0.101 − 0.020 \times L_{CB} + 0.462 \times \Delta$DBH$ + 0.031 \times (L_{CB} \times \Delta$DBH$)$.
The random effects were tree identification number 'ID' and calendar year 'Y' (19 years from 1977–1978 to 1995–1996), the results of which are presented in Table S2 available as Supplementary Data at *Tree Physiology* Online.

Table 2. Results of fixed effects of the linear mixed model shown in Figure 4d. The response variable was the annual growth rate of the stem cross-sectional area (ΔA, cm^2 year^{-1}) at a given stem location on a tree. The fixed effects of explanatory variables are stem length from crown base (L_{CB}, m) and annual growth rate of ABH (the stem cross-sectional area at 1.3-m height) (ΔABH, cm^2 year^{-1}).

Explanatory variable	Estimate	Standard error	t value
(a) Region within the crown			
Intercept	1.465	0.176	8.34
Length from crown base (L_{CB})	0.031	0.031	1.01
ABH growth rate (ΔABH)	0.359	0.028	12.83
$L_{CB} \times \Delta$ABH	0.074	0.004	16.71

AIC of the selected model was 22,281, which was lower than that of the second-best model by ΔAIC = 39. Total number of data points was 7071.

(b) Region below the crown			
Intercept	1.109	0.100	11.05
Length from crown base (L_{CB})	−0.161	0.012	−13.36
ABH growth rate (ΔABH)	0.396	0.024	16.16
$L_{CB} \times \Delta$ABH	0.054	0.003	21.57

AIC of the selected model was 32,617, which was lower than that of the second-best model by ΔAIC = 5. Total number of data points was 10,098.

Using the estimates above, the equations for the lines in Figure 4d are expressed as follows:
Region within the crown: $\Delta A = 1.465 + 0.031 \times L_{CB} + 0.359 \times \Delta$ABH$ + 0.074 \times (L_{CB} \times \Delta$ABH$)$.
Region below the crown: $\Delta A = 1.109 − 0.161 \times L_{CB} + 0.396 \times \Delta$ABH$ + 0.054 \times (L_{CB} \times \Delta$ABH$)$.
The random effects were tree identification number 'ID' and calendar year 'Y' (19 years from 1977–1978 to 1995–1996), the results of which are presented in Table S3 available as Supplementary Data at *Tree Physiology* Online.

indicates that the rate of crown-base rise exceeded the height growth rate, as long as the top of the tree was not broken during growth. In addition, as shown by the colors of the symbols, relatively tall trees in the initial year tended to increase their crown length more by the final year.

Figure 5b illustrates that trees that initially had a greater crown-base diameter (D_{CB21}) gained more D_{CB} by the final year (D_{CB40}), and these trees also initially had a longer crown length, as indicated by the colors of the symbols. The slope of the regression line was significantly greater than unity ($P < 0.05$). Furthermore, of the 50 dying trees (open symbols), 40

experienced a decrease in D_{CB} before they died (one-tailed binomial test: $P < 0.001$), suggesting a decrease in the amount of leaves per tree for the dying trees.

The time-trajectory of the relationship between crown-base diameter (D_{CB}) and crown length (CL) for each tree was also investigated (Figure 5c). As the significant correlation ($P < 0.01$; see Figure 5c legend) between D_{CB} and CL suggests, an occasional decrease in crown length tended to be accompanied by an occasional decrease in crown-base diameter. In particular, among the trees that survived during the observation period (gray line followed by a blue line), the trajectories of the trees
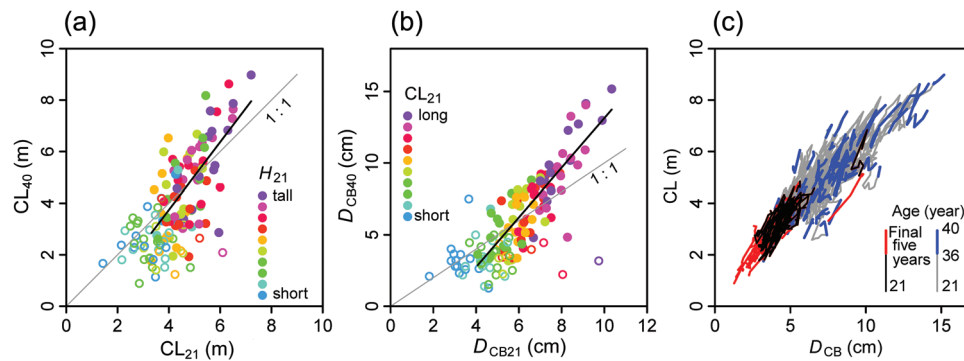
Figure 5. Changes with age in crown length (CL) and crown-base diameter (D_{CB}) of all trees between the ages of 21 and 40 years. (a) Comparison of CL between 21 (CL_{21}) and 40 (CL_{40}) years of age; (b) comparison of D_{CB} between 21 (D_{CB21}) and 40 (D_{CB40}) years of age. Trees were sorted into 10 ranks according to (a) tree height at 21 years old (H_{21}) and (b) crown length at 21 years old (CL_{21}), respectively, as shown by the different colored symbols. Trees that died before 40 years of age (the dying trees) are represented by open symbols, and their values of CL_{40} and D_{CB40} are the crown length 1 year before their death. Regression lines include only the surviving trees in (a) $CL_{40} = -1.51 + 1.31 \times CL_{21}$ (df = 90, F = 66.99, $P < 0.001$, $R^2 = 0.420$) and in (b) $D_{CB40} = -4.19 + 1.73 \times D_{CB21}$ (df = 90, F = 191.4, $P < 0.001$, $R^2 = 0.677$). Symbols lying above the 1 : 1 line (gray line) indicate that the value at 40 years of age was greater than the value at 21 years. (c) Time trajectory of crown-base diameter–crown length (D_{CB}–CL) relationship for all trees. Gray lines with blue lines represent trees that survived between the ages of 21 and 40 years (92 trees in total). The blue lines show the trajectory from 36 to 40 years of age. Black lines with red lines indicate the dying trees (50 trees; 2 trees that died because of breakage in the upper part of the stem, nos. 98 and 144 in Supplementary PDF 1 available as Supplementary Data at *Tree Physiology Online*, are not shown). The red lines denote the trajectory of the final 5 years before the trees' deaths, so that the end point of each red line was <40 years old. When all data were pooled, the correlation was significant ($n = 2376$, $P < 0.001$, $R = 0.907$).
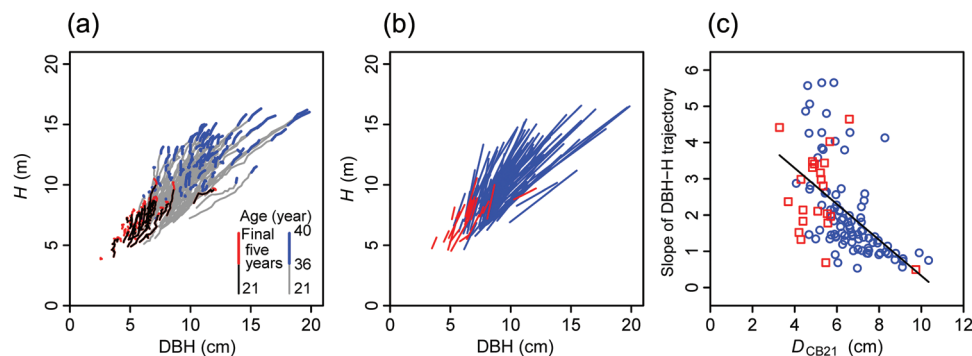

Figure 6. Time trajectories of the DBH–*H* relationship of each tree and its relationship with crown-base stem diameter. (a) DBH–*H* time-trajectory of each tree. Line colors are the same as those in Figure 5c. (b) Regression approximating the DBH–*H* trajectories in (a). Blue lines show regressions for surviving trees and red lines show the dying trees when they were still alive. Regression lines are shown only when significant at $P < 0.05$. Regression analyses were not conducted for trees if the number of data points to be fitted for a tree was two or less. (c) Relationship between the slope (*S*) of the regressions of DBH–*H* trajectories in (b) and the crown-base diameter at 21 years old D_{CB21}. The regression line was $S = 5.27 - 0.49 \times D_{CB21}$ (df = 112, F = 49.27, $P < 0.001$, $R^2 = 0.299$). Blue circles show surviving trees and red squares show the dying trees.

in the middle range of D_{CB} values show an occasional zig-zag pattern of changes in D_{CB} and CL. The dying trees (black lines followed by red lines) consistently experienced a decrease in both crown-base diameter and crown length just before their death, as shown by the clusters of red-line segments (5 years to death) in the lower-left portion of the figure. This suggests that a decrease in crown length is accompanied by a decrease in D_{CB} or in the amount of leaves on a tree.

Time trajectory of DBH–H relationship for each tree

The variation in DBH growth among all trees was examined in terms of the time trajectory of the DBH–*H* relationship (Figure 6a). Trees with taller *H* and thicker DBH, 40 years old,

displayed almost linear DBH–*H* trajectories. In contrast, before the dying trees died (black with red lines), they either exhibited steep trajectories or DBH was asymptotic against tree height. These results indicate that height growth tended to continue even when the DBH growth was weak.

A comparison of the dying trees in Figure 6a with those in Figure 5c suggests that trees with a steep DBH–*H* trajectory (Figure 6a) exhibited decreasing values of CL and D_{CB}. In fact, when the slope of the DBH–*H* trajectory of each tree in Figure 6a is represented by the slope (*S*) of the linear regression between DBH and *H* (Figure 6b), the slope shows a significant negative linear relationship with D_{CB} in the initial year, D_{CB21} ($P < 0.001$; Figure 6c). This result suggests that trees

with a steeper slope for their DBH–H trajectory had a lower amount of leaves in the initial year.

Discussion

DBH–H relationships among trees and the time trajectory of the DBH–H relationship of a tree

By analyzing stem growth patterns of the regions within the crown and below the crown separately, we were able to determine patterns of diameter growth and cross-sectional growth along a stem (Figure 4), as previously summarized by Larson (1963) (see the Introduction). However, despite the trend of ΔD to increase upwards from breast height in the region below the crown (Figure 4c), the variation in ΔD values along a stem was not as large as the variation among trees with different levels of ΔDBH (Figures 2b, 4a and c, Table 1b). In this sense, the ΔDBH of a tree in a given year can be regarded as a representation of diameter growth in the region below the crown in the same year (except for butt swell).

We also demonstrated that long-term patterns of crown-base rise varied among trees (Figure 5a and b), and that this variation was closely connected with the long-term pattern of change in individual crown length: crown length increased in some trees but decreased in others. More importantly, long-term changes in crown length were likely accompanied by long-term changes in the amount of leaves on a tree as suggested by D_{CB} in Figure 5c. Again, some trees showed increased D_{CB}, whereas in others D_{CB} decreased and the trees died. This difference between individual trees illustrates a concrete mechanism of how the sum of A_{CB} in the stand (an index of the leaf area in the stand) could vary only slightly during the

20-year observation period (ranging between 21.0 and 22.9 m² ha⁻¹; see Table S1 available as Supplementary Data at *Tree Physiology* Online), under the presence of both dominant trees increasing their leaf amounts and the constant occurrence of tree death (Table S1 available as Supplementary Data at *Tree Physiology* Online). The amount of leaves on a tree was likely to be a strong regulator of ΔDBH (Figure 3b) and of ΔD values below the crown base (Figure 4a and c), given the similarity between ΔDBH and the ΔD values. Hence, it follows that the DBH growth of a tree had a close connection with the process of crown-base rise, as long-term changes in the amount of leaves were affected by the speed of crown-base rise. This conclusion is important in interpreting the variation in DBH–H trajectory among trees.

From Figure 6, we can infer the relationship between the static DBH–H allometry and the DBH–H trajectory of each individual tree. While the trajectories of the most vigorously growing trees indicated an almost linear increase in both DBH and H, trees with a declining DBH growth rate exhibited an asymptotic tendency towards height growth (Figure 6a). Because the heights of trees with a declining DBH growth rate were short, the static DBH–H allometry at a given point in time may appear to indicate that tree heights were asymptotic against DBH (see the schema in Figure 7). The dying trees were plotted in the lower left part of a static allometry (Figure 6a), and gradually disappeared from the DBH–H plane due to the continual occurrence of tree death. Therefore, the lower-left end of a static allometry will be continually truncated because of the death of suppressed trees. As a result, a static allometry shifts towards the upper-right direction of the DBH–H plane over time (Figure 7). The death of the dying trees suggests that the convexity of a static DBH–H allometry
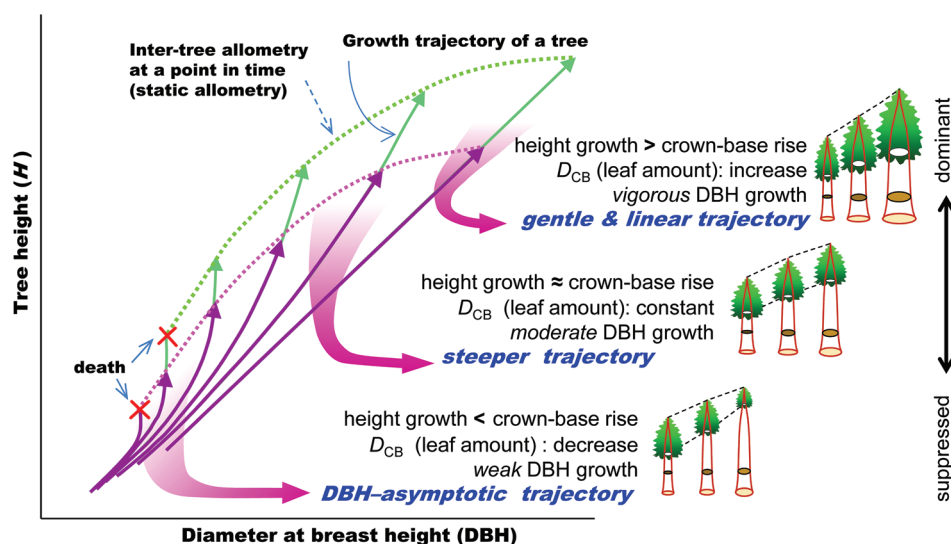

Figure 7. The relationship between the DBH–H trajectories of individual trees and static stem DBH–H allometry in relation to different long-term patterns of change in the crown-base diameter. Note that this schema is based on the results of our even-aged stand (20–40 years old) in which the height of the largest trees continued to increase.

is affected by the susceptibility to death or shade tolerance in the declining trees.

The relationship between the static allometry and DBH–H trajectories of individual trees (Figure 6a) is similar to the relationship reported for annual plants (Weiner and Thomas 1992, Nagashima and Terashima 1995). In the present study, we demonstrated that in tree species, stem thickness growth (ΔDBH) is likely to be affected by the amount of leaves per tree (Figure 3b). The steep slope of the DBH–H trajectory could be attributed to a progressively decreasing amount of leaves over time. Further studies are needed to determine if the results here relating to the amount of leaves also apply to annual plants.

Interpretation of height growth and crown-base rise—the 'leaf-turnover priority' hypothesis

From an ecological viewpoint, continued height growth of trees at the expense of diameter growth under suppressed conditions is considered a response to obtain better light conditions (Kohyama 1987). However, this notion of the 'priority of height growth' does not represent the growth of trees appropriately, as we have demonstrated that even dying trees with $\Delta D \approx 0$ in the region below the crown maintained $\Delta D > 0$ within the crown, until about 5 years before death, with height growth being continued to some extent (Figure 6a). These results suggest that the significance of the 'priority of height growth' is likely to be better understood by considering it as the priority of stem growth in the region within the crown than in the region below the crown.

Note here that height growth, the elongation of the top shoot within the crown, could be accompanied by the elongation of other lateral shoots, on which new leaves are produced. Because new leaves are generally produced during annual-shoot growth (e.g., Kozlowski and Pallardy 1997, Beck 2005), the length of an annual shoot is positively related to the number of leaves or leaf area on a shoot in tree species (Yagi and Kikuzawa 1999, Sumida and Takai 2003). This is especially true for tree species that do not form short shoots, such as C. obtusa. New-leaf production is known to be most active in the uppermost part of a coniferous crown (Kurachi et al. 1986). These previous findings suggest that height growth is likely to represent the activity of new-leaf production of an individual. More importantly, because an evergreen leaf has longevity, a tree must turn over leaves to survive even if the tree is growing under suppressed conditions. The stand-mean leaf turnover time of the study plot was estimated to be between 4.3 and 6.3 years based on the ratio of the amount of leaves to the leaf-litterfall rate (Miyaura 1989). In addition, the crown-base rise found in this study implies that leaves in the lower crown were lost due to leaf death, meaning that continual new-leaf production is essential for the maintenance of photosynthesis, irrespective of the causes of leaf death in the lower crown. In response to new-leaf production (primary growth), stem diameter growth (secondary growth) would occur within the crown. This would allow newly produced leaves to secure conductive tissues (Spicer and Groover 2010). It is therefore likely that the priority of growth within the crown corresponds to the need for leaf turnover. We refer to this as 'the leaf-turnover priority hypothesis' to explain the ecological significance of height growth.

This hypothesis also accords with the previously described relationship between radial growth and hormonal activities (e.g., Funada et al. 1989, Funada et al. 2001). Indole-3-acetic acid, an auxin known to be responsible for secondary cambial growth (Sundberg et al. 1993, Uggla et al. 1996), is synthesized in buds and young shoots (Odani 1985, Uggla et al. 1998). This suggests that, even in declining trees, some radial growth within the crown should occur as long as new leaves are produced, as indicated by the results of the present study. Hence, hormonal activities provide a likely physiological mechanism for the maintenance of diameter growth rates at a certain level within the crown, even in declining trees.

The mechanism suggested above accounts not only for stem growth in the region within the crown but also for growth below the crown. In dominant trees with increasing amounts of leaves (e.g., tree no. 101 in Figure 1a), stem growth below the crown can be interpreted as the increase in sapwood area in the region below the crown necessary to sustain the increasing amount of leaves (increasing D_{CB}). Conversely, suppressed trees with decreasing amounts of leaves may not have to increase their sapwood area in the region below the crown if the existing sapwood area below the crown is sufficient. This is suggested by tree no. 114 (Figure 1c), of which the amount of leaves was decreasing (decreasing D_{CB}). The diameter of this tree at 6.3 m height increased by as much as 2.8 cm during the first 10 years when this stem height was within the crown. After the point located at 6.3 m became positioned below the crown, an increase of only 0.6 cm occurred during the following 9 years. The DBH (1.3 m height in Figure 1c) increased by only 0.8 cm during the 19-year period from the ages of 21 to 40 years old. A sudden decrease in ring width on a given stem cross section (as at the 6.3 m stem height) may occur simply by the transition of that location from within the crown to below the crown, without sudden changes in light conditions or sudden suppression by neighboring crowns. The physiological reason for the discrepancy between the regions within and below the crown is explained by the discussion above.

The hypothesis of leaf-turnover priority further explains how trees die as a consequence of competition. We demonstrated that prior to the actual death of the dying trees, their crown lengths declined due to rapid crown-base rise, accompanied by a reduction in D_{CB} (Figure 5) and hence a reduction in the amount of leaves. Little height growth occurred during the final 5 years before death in the dying trees (Figure 6a). These

results suggest that the dying trees produced very few new leaves just before the death of an individual. Older leaves in the lower region of crowns would have gradually died due to old age and/or continued suppressed conditions. Thus, the leaf-turnover hypothesis explains why crown-base rise occurs (Sprugel 2002), why trees lose their leaves, and why trees die as a consequence of competition. Crown-base rise and the associated change in the amount of leaves with growth can occur in some hardwood species (Sumida and Komiyama 1997). The hypothesis may therefore also apply to hardwood species.

In addition, we should consider several features that might be specific to this study in our discussion of the DBH–H relationship and the leaf-turnover priority hypothesis. Our observations were made during stages of relatively vigorous growth (up to 40 years old) in which the height growth of the tallest trees was not declining. However, *C. obtusa* can live >300 years and the maximum tree height reaches >30 m in native conditions (see Materials and methods). The stems of mature, old trees of many species often have a blasted-out top (Van Pelt 2001), but such old trees often maintain their crown and foliage via constant, repeated formation and death of epicormic shoots (Ishii and Ford 2001, Ishii et al. 2002), and maintain stem wood production (Sillett et al. 2010). Clearly, leaf turnover does not always have to accompany crown rise. In addition, characteristics of *C. obtusa*, such as its shade-tolerant foliage and crown composed of dense branches that do not form branch whorls, might have contributed to the relatively continuous crown-base rise seen in this study. Further studies are necessary to confirm the validity and relevance of this hypothesis.

Conclusion

We have confirmed that the crown base is a practical border of diameter growth patterns along the stem. We have further shown how crown-base rise is relevant for understanding the process of stem shape formation, death of trees in a competitive environment, variations in the DBH–H time-trajectory among trees and the long-term change in static DBH–H allometry. In particular, the view that crown-base rise is strongly related to leaf-turnover status aids in interpreting DBH–H relationships. These results are also important for studies in other areas. For example, stem thickening and stem elongation are affected by external mechanical forces and stimuli at different scales (e.g., Jaffe 1973, Morgan and Cannell 1994, Mattheck 1998, Chehab et al. 2009), but this may not necessarily mean that a stem shape acquired in a closed stand is due solely to the thickening pattern predicted by a particular theory of stem shape formation. Effects of transfer from the region within the crown to the region below the crown at a given stem height should be considered when stem shape is acquired in a stand.

As another example, the patterns of diameter/cross-sectional area growth rates along a stem, as we showed in relation to crown-base rise patterns, can provide important information for studies of the distribution of respiration rates along a stem (e.g., Araki et al. 2010) because total stem respiration increases due to growth respiration, the respiration associated with stem growth (Adu-Bredu et al. 1996).

We also demonstrated that DBH growth was not always concordant with diameter growth within the crown. This might be a reason for the reported inconsistencies between DBH growth and biomass increment (Bouriaud et al. 2005, Sillett et al. 2010) and would be worth considering in future studies of the stem volume, biomass and productivity of forests.

We used the crown-base diameter (D_{CB}) and cross-sectional area (A_{CB}) as surrogates for the amount of leaves on a tree, assuming that the pipe–model relationship established for the study forest (Miyaura 1989, Hagihara et al. 1993) applied to all trees and all years. The analysis results showed that the amount of leaves on a tree increases or decreases in accordance with the vigor of diameter growth. Long-term changes in the amount of leaves on a tree were also likely to accompany an increase or decrease in crown length. These stem growth patterns conform to reported patterns of the relationships between IAA activity and stem growth rates. Our results further suggest that the maintenance of the crown, for which leaf turnover is indispensable, is important for determining the growth of trees in a community. To summarize, the results of our analyses using information regarding the crown base have relevance to studies of stem-shape formation, the location of hormonal activities and cambial growth along the stem, and physiological and ecological constraints relating to leaf turnover and their relationships with the survival/death of trees under competition.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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References

Adu-Bredu S, Yokota T, Hagihara A (1996) Carbon balance of the aerial parts of a young hinoki cypress (*Chamaecyparis obtusa*) stand. Tree Physiol 16:239–245.

Araki MG, Utsugi H, Kajimoto T, Han Q, Kawasaki T, Chiba Y (2010) Estimation of whole-stem respiration, incorporating vertical and seasonal variations in stem CO_2 efflux rate, of *Chamaecyparis obtusa* trees. J For Res Jpn 15:115–122.

Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using S4 classes. R package version 0.999375-41. http://CRAN.R-project.org/package=lme4 (23 November 2011, date last accessed).

Beck CB (2005) An introduction to plant structure and development. Cambridge University Press, Cambridge, 431 pp.

Bouriaud O, Bréda N, Dupouey J-L, Granier A (2005) Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. Can J For Res 35:2920–2933.

Chehab EW, Eich E, Braam J (2009) Thigmomorphogenesis: a complex plant response to mechano-stimulation. J Exp Bot 60:43–56.

Chiba Y (1990) Plant form analysis based on the pipe model theory I. Statical model within the crown. Ecol Res 5:207–220.

Chiba Y, Fujimori T, Kiyono Y (1988) Another interpretation of the profile diagram and its availability with consideration of the growth process of forest trees. J Jpn For Soc 70:245–254.

Courbet F, Houllier F (2002) Modelling the profile and internal structure of tree stem. Application to *Cedrus atlantica* (Manetti). Ann For Sci 59:63–80.

Faraway JJ (2006) Extending the linear model with R. Chapman & Hall/CRC, Boca Raton, 301 pp.

Funada R, Kubo T, Fushitani M (1989) Vertical distribution of annual ring characteristics in relation to the crown profile in Akamatsu (*Pinus densiflora*). Mokuzai Gakkaishi 35:944–947.

Funada R, Kubo T, Tabuchi M, Sugiyama T, Fushitani M (2001) Seasonal variations in endogenous indole-3-acetic acid and abscisic acid in the cambial region of *Pinus densiflora* Sieb. et Zucc. stems in relation to earlywood–latewood transition and cessation of tracheid production. Holzforschung 55:128–134.

Gray HR (1956) The form and taper of forest-tree stems. Imperial Forestry Institute Paper no. 32. Oxford University Press, Oxford, UK, pp 1–79.

Hagihara A, Suzuki M, Hozumi K (1978) Seasonal fluctuations of litterfall in a *Chamaecyparis obtusa* plantation. J Jpn For Soc 60:397–404.

Hagihara A, Yokota T, Ogawa K (1993) Allometric relations in Hinoki (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) trees. Bull Nagoya Univ For 12:11–29.

Hara T, Kimura M, Kikuzawa K (1991) Growth patterns of tree height and stem diameter in populations of *Abies veitchii*, *A. mariesii* and *Betula ermanii*. J Ecol 79:1085–1098.

Hayashi Y (1985) Woody plants of Japan. Yama-kei Publishers, Tokyo, 752 pp (in Japanese).

Henry HAL, Aarssen LW (1999) The interpretation of stem diameter–height allometry in trees: biomechanical constraints, neighbor effects, or biased regressions? Ecol Lett 2:89–97.

Hoshino D, Nishimura N, Yamamoto S (2001) Age, size structure and spatial pattern of major tree species in an old-growth *Chamaecyparis obtusa* forest, Central Japan. For Ecol Manag 152:31–43.

Ishii H, Ford ED (2001) The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* (Douglas-fir) trees. Can J Bot 79:251–264.

Ishii H, Ford ED, Dinnie E (2002) The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* (Douglas-fir) trees II. Basal reiteration from older branch axes. Can J Bot 80:916–926.

Iida Y, Kohyama TS, Kubo T, Kassim AR, Pooter L, Sterck F, Potts MD (2011) Tree architecture and life-history strategies across 200 co-occurring tropical tree species. Funct Ecol 25:1260–1268.

Ilomäki S, Nikinmaa E, Mäkelä A (2003) Crown rise due to competition drives biomass allocation in silver birch. Can J For Res 33:2395–2404.

Jaffe MJ (1973) Thigmomorphogenesis: the response of plant growth and development to mechanical stimulation with special reference to *Bryonia dioica*. Planta 114:143–157.

King DA, Davies SJ, Tan S, Md Noor NS (2009) Trees approach gravitational limits to height in tall lowland forests of Malaysia. Funct Ecol 23:284–291.

Kitamura S, Murata G (1979) Colored illustrations of woody plants in Japan. Vol. II. Hoikusha Publishing, Osaka, 545 pp (in Japanese).

Kohyama T (1987) Significance of architecture and allometry in saplings. Funct Ecol 1:399–404.

Kohyama T, Hara T, Tadaki Y (1990) Patterns of trunk diameter, tree height and crown depth in crowded *Abies* stands. Ann Bot 65:567–574.

Kurachi N, Hagihara A, Hozumi K (1986) Distribution of leaf and branch-biomass density within a crown of Japanese larch and its relationship to primary production: analysis by Sainome cutting. In: Fujimori T, Whitehead D (eds) Crown and canopy structure in relation to productivity. Forestry and Forest Products Research Institute, Ibaraki, Japan, pp 308–322.

Kozlowski TT, Pallardy SG (1997) Physiology of woody plants. Academic Press, San Diego, CA, 411 pp.

Larson PR (1963) Stem form development of forest trees. For Sci 9 (Monograph 5):1–42.

Mäkelä A (2002) Derivation of stem taper from the pipe theory in a carbon balance framework. Tree Physiol 22:891–905.

Mäkelä A, Valentine HT (2006) Crown ratio influences allometric scaling in trees. Ecology 87:2967–2972.

Mattheck C (1998) Design in nature. Springer, Berlin, 276 pp.

McMahon TA (1975) The mechanical design of trees. Sci Am 233:92–102.

Miyaura T (1989) Studies on litterfall of forest trees. PhD thesis, Nagoya University, Nagoya, Japan, 246 pp (in Japanese).

Miyaura T, Hozumi K (1982) Nondestructive measurements of *Chamaecyparis obtusa* plantation (III). Transactions of the 93rd Annual Meeting of the Japanese Forestry Society, pp 343–344 (in Japanese).

Miyaura T, Hozumi K (1985) Measurement of litterfall in a Hinoki (*Chamaecyparis obtusa* S. et Z.) plantation by the clothing-trap method. J Jpn For Soc 67:271–277.

Morgan J, Cannell MGR (1994) Shape of tree stems—a re-examination of the uniform stress hypothesis. Tree Physiol 14:49–62.

Nagashima H, Terashima I (1995) Relationships between height, diameter and weight distributions of *Chenopodium album* plants in stands: effects of dimension and allometry. Ann Bot 75:181–188.

Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol Monogr 76:521–547.

Niklas KJ (1995) Size-dependent allometry of tree height, diameter and trunk-taper. Ann Bot 75:217–227.

Nilsson J, Karlberg A, Antti H, Lopez-Vernaza M, Mellerowicz E, Perrot-Rechenmann C, Sandberg G, Bhalerao RP (2008) Dissecting the

molecular basis of the regulation of wood formation by auxin in hybrid aspen. Plant Cell 20:843–855.

Odani K (1985) Indole-3-acetic acid transport in pine shoots under the stage of true dormancy. J Jpn For Soc 67:332–334.

Oliver CD, Larson BC (1996) Forest stand dynamics. John Wiley & Sons, New York, 520 pp.

Oohata S, Shinozaki K (1979) A statistical model of plant form—further analysis of the pipe model theory. Jpn J Ecol 29:323–335.

Osawa A (1990) Reconstructed development of stem production and foliage mass and its vertical distribution in Japanese larch. Tree Physiol 7:189–200.

Osawa A, Ishizuka M, Kanazawa Y (1991) A profile theory of tree growth. For Ecol Manag 41:33–63.

Osunkoya OO, Omar-Ali K, Amit N, Dayan J, Daud DS, Sheng TK (2007) Comparative height–crown allometry and mechanical design in 22 tree species of Kuala Belalong rain forest, Brunei, Borneo. Am J Bot 94:1951–1962.

Paembonan SA, Hagihara A, Hozumi K (1990) Photosynthesis of a Hinoki tree. Transactions of the 38th Annual Meeting of the Chubu Branch of the Japanese Forestry Society, pp 63–66.

Phillips R (1978) Trees in Britain. Pan Books, London, 224 pp.

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/ (23 November 2011, date last accessed).

Shinozaki K, Yoda K, Hozumi K, Kira T (1964a) A quantitative analysis of plant form—the pipe model theory I. Basic analysis. Jpn J Ecol 14:97–105.

Shinozaki K, Yoda K, Hozumi K, Kira T (1964b). A quantitative analysis of plant form—the pipe model theory II. Further evidence of the theory and its application in forest ecology. Jpn J Ecol 14:133–139.

Sillett SC, Van Pelt R, Koch GW, Ambrose AR, Carroll AL, Antoine ME, Mifsud BM (2010) Increasing wood production through old age in tall trees. For Ecol Manag 259:976–994.

Spicer R, Groover A (2010) Evolution of development of vascular cambia and secondary growth. New Phytol 186:577–592.

Sprugel DG (2002) When branch autonomy fails: Milton's law of resource availability and allocation. Tree Physiol 22:1119–1124.

Sterck FJ, Bongers F (1998) Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. Am J Bot 85:266–272.

Sumida A, Komiyama A (1997) Crown spread patterns for five deciduous broad-leaved woody species: ecological significance of the retention patterns of larger branches. Ann Bot 80:759–766.

Sumida A, Takai Y (2003) Formation of a structure of exponentially forking branches with a steady-state amount of current-year shoots in a hardwood tree crown. In: Sekimura T, Noji S, Ueno N, Maini PK (eds) Morphogenesis and pattern formation in biological systems: experiments and models. Springer, Tokyo, pp 247–256. http://hdl. handle.net/2115/44835 (23 November 2011, date last accessed).

Sumida A, Ito H, Isagi Y (1997) Trade-off between height growth and stem diameter growth for an evergreen oak, Quercus glauca, in a mixed hardwood forest. Funct Ecol 11:300–309.

Sumida A, Nakai T, Yamada M, Ono K, Uemura S, Hara T (2009) Ground-based estimation of leaf area index and vertical distribution of leaf area density in a Betula ermanii forest. Silva Fenn 43:799–816.

Sundberg B, Ericsson A, Little CHA, Näsholm T, Gref R (1993) The relationship between crown size and ring width in Pinus sylvestris L. stems: dependence on indole-3-acetic acid, carbohydrates and nitrogen in the cambial region. Tree Physiol 12:347–362.

Uggla C, Moritz T, Sandberg G, Sundberg B (1996) Auxin as a positional signal in pattern formation in plants. Proc Natl Acad Sci USA 93:9282–9286.

Uggla C, Mellerowicz EJ, Sundberg B (1998) Indole-3-acetic acid controls cambial growth in Scots pine by positional signaling. Plant Physiol 117:113–121.

Van Laar A, Akça A (2007) Forest mensuration. Springer, Dordrecht, 383 pp.

Van Pelt R (2001) Forest giants of the pacific coast. University of Washington Press, Seattle, 200 pp.

Valentine HT, Gregoire TG (2001) A switching model of bole taper. Can J For Res 31:1400–1409.

Valentine HT, Mäkelä A (2005) Bridging process-based and empirical approaches to modeling tree growth. Tree Physiol 25:769–779.

Valentine HT, Ludlow AR, Furnival GM (1994) Modeling crown rise in even-aged stands of Sitka spruce or loblolly pine. For Ecol Manag 69:189–197.

Valentine HT, Mäkelä A, Green EJ, Amateis RL, Mäkinen H, Ducey MJ (2012) Models relating stem growth to crown length dynamics: application to loblolly pine and Norway spruce. Trees Struct Funct 26:469–478.

Weiner J, Thomas SC (1992) Competition and allometry in three species of annual plants. Ecology 73:648–656.

West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. Science 276:122–126.

Yagi T, Kikuzawa K (1999) Patterns in size-related variations in current-year shoot structure in eight deciduous tree species. J Plant Res 112:343–352.